

RESEARCH PAPER

Hydraulic resistance components of mature apple trees on rootstocks of different vigours

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Abstract

Dwarfing of fruit trees is often achieved through the use of dwarfing rootstocks. Dwarf trees are characterized by sustained reductions in vegetative growth during the lifetime of the tree. The dwarfing mechanism is not well understood, but it has been hypothesized that hydraulic properties of the rootstock and the graft union are involved. It is hypothesized here that leaf- or stem-specific resistance of at least one hydraulic component of the water transport system would be negatively correlated with rootstock 'vigour', and this could be useful for selection of rootstocks. Hydraulic resistance (R) of fully grown apple trees on a variety of rootstocks of different 'vigours' was measured. Most measurements were with the evaporative flux (EF) method, where water uptake measured with sap flow sensors was related to the pressure gradient from soil (taken as pre-dawn leaf) and midday root (taken as covered root-sucker), stem (from covered leaf), and exposed and shaded leaf water potentials (Ψ). R of trees on dwarfing M9 rootstock was compared with that of more vigorous MM106 and MM111 rootstocks in Israel and Vermont, USA. In Israel, M9 consistently had higher leaf-specific hydraulic resistance (R_l) in the soil to scion stem pathway, but this difference was only significant for one summer. R was larger in M9 between the root and stem, implicating the graft union as the site of increased resistance. In Vermont, R_l of 9- and 10-year-old trees on six rootstocks of various vigours was not consistently related to vigour, and stem-specific resistance (R_s) increased with increasing

vigour. High pressure flow meter (HPFM) measurements gave a lower R than the EF method in all but one case, perhaps indicating a significant amount of xylem dysfunction in these trees, and demonstrated the increased resistivity of stem sections that included dwarf graft unions as compared with non-graft stem sections. It is concluded that stem- and leaf-specific R are not consistently positively correlated with dwarfing, although the increased resistivity of the graft union in dwarfing rootstocks may influence the transport of water and other elements across the graft union, and therefore be involved in the dwarfing mechanism.

Key words: Conductance, dwarfing, graft union, *Malus domestica*, scion.

Introduction

Rootstocks can bestow specific properties on the tree. One of the more important properties in modern orchards is a sustained reduction in vegetative growth rates, or 'dwarfing'. Several studies have hypothesized that 'dwarfing' by rootstocks results from an increase in leaf-specific hydraulic resistance (R_l), which causes reductions in canopy water status and in rates of gas exchange and subsequent growth (Kamboj *et al.*, 1997) or changes in diurnal water potential variations that are related to shoot elongation (Basile *et al.*, 2003a). There is practical importance to this hypothesis, since breeders would like to be able to determine a rootstock's vigour from physiological parameters, instead of arduous long-term trials.

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Studies of dwarfing rootstocks in apple trees have found evidence for increased R (Olien and Lakso, 1984, 1986; Higgs and Jones, 1990). Measurements have shown that sites of increased R may be the root system (Syvertsen, 1981, for citrus; Basile *et al.*, 2003b, for peach; Nardini *et al.*, 2006, for olive) or the graft union region (Cohen and Naor, 2002; Atkinson *et al.*, 2003, for apples; Olmstead *et al.*, 2006, for cherry). Apple and pome fruit studies that actually measured R each targeted only two or three rootstocks, and no information is available on other rootstocks. In addition, Cohen and Naor (2002) were not able to measure the graft union region, and Atkinson *et al.* (2003) measured only a few parts of young plants. These deficiencies leave room for more focused study.

R expresses the water potential (Ψ) gradient necessary to cause unit water flux. Since the size of the Ψ gradient is limited to potentials that maintain the integrity of the water columns in the xylem, R and the maximum Ψ gradient define the maximum rate of water transport in the tree. This rate also determines what maximum leaf conductance to water vapour and CO_2 uptake can be attained for a given amount of leaf area. Thus, for a given leaf area and Ψ gradient, tree gas exchange is limited by R .

There is more than one possibility for an influence of R and its reciprocal, conductance, on growth rates of the scion. One direct mechanism is via gas exchange and subsequent productivity. Such a mechanism, and the theoretical connection between R_1 , canopy conductance, and photosynthesis, has been discussed elsewhere (Sperry, 2000; Cohen and Naor, 2002). Cohen and Naor (2002) found that differences in leaf-specific hydraulic conductance between vigorous and weak rootstocks were accompanied by differences in canopy conductance, but no consistent differences in porometer measurements of leaf conductance or carbon 13 isotopic ratios were found (Cohen *et al.*, 2003). Similarly, Clearwater *et al.* (2004) did not find a direct relationship between dwarfing and whole plant hydraulic conductance, water status, and photosynthesis in vigour-controlling kiwifruit (genus *Actinidia*) rootstocks. Nardini *et al.* (2006) compared one dwarfing with one vigorous rootstock in olive trees and found that the reduced total hydraulic conductance of the root system of the dwarfing rootstock was comparable with the reduction in leaf area of the scion even though differences in leaf-specific resistance were minor. They concluded that in this case hydraulics could explain dwarfing, since the canopy size was coupled to root conductance. Gasco *et al.* (2007), working with the same olive rootstocks, found that the resistance of the graft union comprises a significant part of the total resistance only during the first 2 months. Thus, sustained differences in scion vegetative growth could not be explained by differences in the graft union. Clearwater *et al.* (2006) found that kiwifruit dwarfing is related to differences in early season canopy development, and suggested that

differences in hydraulic conductance at that time may lead to dwarfing, while most evaluations of hydraulic conductance have been made after full canopy development. Another proposed mechanism for the hydraulic influence of rootstocks is that diurnal variations in stem water potential modulate stem elongation (Basile *et al.*, 2003b). The latter was based on the correlation between the rate of change of water potential and stem extension rate in peach trees, as investigated and modelled by Berman and DeJong (1997).

In addition to restriction of water transport, increased R or differences in xylem properties may influence transport of solutes, including nutrients and hormones in the xylem (Lockard and Schneider, 1981). Such influences might be considered to be indirect influences of changes in R . Non-hydraulic mechanisms for dwarfing have also been suggested (Lockard and Schneider, 1981).

Several methods have been used to measure R in trees. All involve measurement of a pressure gradient and the resulting flow rate. The evaporative flux (EF) method determines R *in vivo*. For this method, sap flux and Ψ gradients are monitored. Sap flux and Ψ vary during the day, so assuming that R changes little during the day the average total R might be determined from the linear relationship between sap flux and Ψ (Passioura and Munns, 1984). However, capacitance of the tree, which in large apple trees can amount to 2 h worth of transpiration (Landsberg *et al.*, 1976), causes hysteresis in the relationship, and inaccuracies when Ψ is changing (Moreshet *et al.*, 1990). Nevertheless in summer clear sky conditions, midday sap flux and water potential are usually constant for several hours at midday (Cohen and Naor, 2002; Li *et al.*, 2002), indicating steady-state flow and no capacitance contribution to the EF at that time. If Ψ at different points in the soil–root–stem–leaf continuum is measured at these times, then R can be determined and partitioned (Moreshet *et al.*, 1990). For total plant R , either a leaf Ψ value corresponding to soil–plant equilibrium at zero flow or the soil water potential is needed (i.e. the intercept). The former is the case before dawn, and pre-dawn leaf Ψ has been shown for citrus to be close to the zero intercept of the plot of Ψ on sap flow (Cohen *et al.*, 1983). For these reasons, in the current study the pre-dawn leaf Ψ was taken as a proxy for soil Ψ , which for non-dry soil was assumed to remain constant during the day. Additional points used for partitioning R are stem Ψ , taken from measurements of covered leaves (Naor *et al.*, 1995; Jones, 2004), and large root Ψ , taken from covered leaves on root suckers (Simonneau and Habib, 1991).

A direct R measurement technique is with a high pressure flow meter (HPFM; Tyree *et al.*, 1995), in which the plant is severed at a point where a pressure-tight connector can be attached, and pressurized water is forced into the plant while the flow rate is monitored simultaneously. In many cases, this method gives results

comparable with those obtained with the EF method (Tsuda and Tyree, 2000). This method is direct, and can be applied in the field (Basile *et al.*, 2003b), but the pressure applied is enough to hydrate and activate dysfunctional xylem (Sperry *et al.*, 1988), so that the results may underestimate the operational resistance, giving a potential resistance. EF *R* can be several times larger than that obtained with the HPFM, and the difference may give insight into the extent of cavitation and/or xylem dysfunction (Rieger, 1989).

This study investigates the hypothesis that stem- and leaf-specific *R* are correlated with sustained rootstock vigour. A series of field experiments were conducted to determine *R* of full-sized apple (*Malus domestica* Borkh.) trees on seven rootstocks of different vigours. *R* was partitioned into soil–root, soil–stem, root–stem, and stem–leaf components, and resistivity of stem sections with and without graft unions was measured.

Materials and methods

Sites and plant material

The experiments were in apple orchards in Burlington, Vermont, USA and in the highlands of North-Eastern Israel (at Kibbutz Ortal). Details of the different varieties used are given in Table 1, along with some information on their parentage, where available. Trunk cross-sectional area and total leaf area measured on the trees in Vermont in 2002 are also given. Trunk cross-sectional areas, which are used as a relative measure of vigour, confirm that the rootstock classification was roughly correct for conditions in northern Vermont.

Ortal, Israel: Measurements were carried out in a commercial fruit-bearing apple orchard at Kibbutz Ortal (33°05'N; 35°44' E; 900 m above mean sea level) in North-Eastern Israel. Tree scions were of the Golden Delicious 'Smoothie' cultivar on two rootstocks (MM106 and virus-free M9), which in Israel's climate produce

large and medium sized canopies, respectively, 3 years after planting. Trees were planted in 1997 and trained as 'central leader'. Irrigation was daily with an automatic drip system, according to standard commercial practice for the region. Trees were not pruned during the seasons when measurements were made.

Measurements were made in rows of trees in which all trees were of the same rootstock. In each season, eight trees on both MM106 and M9 rootstocks were measured using two sap flow systems. Suckers, i.e. new shoots that grew from the base of the rootstock below the graft, were allowed to develop. Trees were selected for measurement if they had enough sucker leaves for the measurement programme.

Burlington, USA: Measurements were carried out in the University of Vermont's (UVM) horticultural research centre in Burlington, VT (44°28'N; 73°9'W; 100 m above mean sea level). Trees were from the NC-140 1992–1993 Liberty/CG Apple Rootstock Trial led by Terence Robinson (see www.nc140.org), which, in Vermont, was an evaluation of several 'M' and 'CG' series rootstocks for the Cornell/Geneva Rootstock Breeding Program with the scab-resistant scion cultivar 'Liberty'. Trees were planted in 1992 in three rows, with each row representing one of the types: dwarf, semi-dwarf, and vigorous. The order of the rootstock varieties varied at random along the row. For the current study, two typical trees of each of the following rootstocks were selected: vigorous M111 and CG934, semi-dwarf M7A and CG30, and dwarf M9 and CG202. This gave a total of 12 trees, but, due to sap flux instrumental limitations, only eight were measured simultaneously. In order to measure all 12, the four trees on the vigorous rootstocks were always measured, and the dwarf and semi-dwarf trees were measured at different times. HPFM measurements were made on a total of eight of these trees in the autumn of 2002 (two M111s, one CG934, one M7A, one CG30, two M9s, and one CG202).

The orchard was rain-fed, since there is usually ample rain in the summer, and supplemental irrigation was supplied with drippers. The summer of 2001 had a drought spell which overlapped with the measurements, during which the orchard was not irrigated regularly. The drought was mild and did not have a visible impact on yields. Measurements were made during the summers of 2001 and 2002. Trees were not pruned during the two years of the experiment. Orchard maintenance included removal of suckers before they could be measured.

Table 1. Descriptive parameters of the rootstocks and trees used in this study

Areas are those of the Liberty scion measured after 11 years, on trees in the rootstock trial in Vermont. For leaf area measurement, see the Materials and methods.

Variety	Type	Size class	Stem area, (m ² ×10 ⁻³)	Leaf area, (m ²)	Parentage/Latin name
M.9-EMLA	Rootstock	3, dwarf	1.6	4.2	Unknown ^b
CG-202	Rootstock	Dwarf	2.9	12.1	
M7a	Rootstock	6, semi-dwarf	2.8	8.4	Unknown, virus reduced clone ^b
CG-30	Rootstock	5–6, semi-dwarf	5.1	23.3	Robusta 5×M.9
MM.106-EMLA	Rootstock	7, semi-vigorous	N/A ^a	N/A	Nothorn Spy×M.1 ^b
MM.111-EMLA	Rootstock	8, vigorous	5.9	12.1	Northern Spy×M.1.793 ^b
CG-934	Rootstock	Vigorous	7.1	10.7	
Golden Delicious	Scion	N/A	N/A	N/A	<i>Malus domestica</i>
Liberty	Scion	N/A	N/A	N/A	<i>Malus domestica</i>

^a N/A not applicable.

^b Source: Cornell University–New York State Agricultural Experimental Research Station, Geneva, NY fact sheet at: <http://www.nysaes.cornell.edu/hort/breeders/appleroots/Factsheets/FSAccess.html>. This web site, which contains additional information on the rootstocks, explains that rootstocks are ranked 'by size class from smallest (1) to largest (10). Size classes are estimated as the relative per cent tree size of an own-rooted (full sized) tree, e.g. size class 1 represents a rootstock that produces a tree 10–20% the size that an own-rooted tree would produce under similar conditions'.

Sap flow

Sap flow measurements were made with the heat pulse technique (for details see Cohen *et al.*, 1981; Cohen, 1994) using custom-made probes, heaters, pulse generators and multiplexers (Ariel Amplifications, Petah Tiqva, Israel), and commercial dataloggers (types CR21X and CR10X; Campbell Scientific, Logan, UT, USA). Each system consisted of eight heater and probe pairs, one pulse generator–multiplexer, and one datalogger. The eight probe pairs were measured sequentially at 7.5 min intervals so that each probe pair was measured once per hour. Each probe pair consisted of a reference probe which measured background sapwood temperature ~ 10 cm below the heater, and a second probe 15 mm above the heater, which contained six microbead thermistors, placed at 8 mm intervals along the probe length. The latter probes and the heaters were inserted into holes drilled in the scion at least 10 cm above the graft, from the south of the tree. Sap flow was measured simultaneously 4, 12, 20, 28, 36, and 44 mm into the sapwood. No consistent pattern in the azimuthal distribution of sap flux has been found in the past in apple trees (Cohen and Naor, 2002). Calibration values and parameters for computing sap flux density were taken from previous work (Cohen *et al.*, 1981; Jones *et al.*, 1988; Cohen, 1994). Holes were drilled using a precision-tooled guide to ensure that heater and probe bores were exactly 15 mm apart and parallel for the full depth of the sensor probe. Distances between probe and heater for deep parts of the bores were checked several times in narrow (< 6 cm diameter) trunks where probe and heater protruded from the opposite side of the trunk. In all cases, the error in distance was < 1 mm.

Leaf water potential Ψ_l

Ψ_l was measured with pressure chambers (PMS Instruments, Corvallis OR, USA and Arimad, Kfar Haruv, Israel). Leaves were cut, immediately bagged in plastic, and then taken to the pressure chamber where they were shaded until measurement within a few minutes. Covered leaves, used for determination of stem Ψ , were covered with aluminium foil either the previous evening or several hours before measurement (Naor, 1998). For measurement of root Ψ , all leaves of suckers were covered the previous day, sucker shoots were shaded with dense reflective shade screens, and individual leaves were measured at midday. Covered leaves were left in their covers until after measurement.

Daily courses of Ψ_l used for computing hydraulic conductance by the EF method started with measurements of pre-dawn Ψ_l , followed by either measurement every 1 h or 1.5 h throughout the day, or measurements made during 3–4 midday hours. Midday Ψ taken for the R computation was the average of the values for 3 h or 4 h when readings of both Ψ and sap flow were stable.

Hydraulic conductance—evaporative flux (EF) method

In this method, flux is monitored together with Ψ along the soil–tree continuum, and R is calculated as the ratio of Ψ gradient to flux. R can then be partitioned into that of the soil to root, root to stem, and stem to leaf pathways (Moreschet *et al.*, 1990; Clearwater *et al.*, 2004). Pre-dawn Ψ_l (Ψ_{pd}) was taken as a proxy for soil Ψ (Cohen *et al.*, 1983); large root Ψ was represented by the xylem Ψ measured on covered leaves of the suckers (Simonneau and Habib, 1991); stem Ψ was measured on covered leaves selected inside the canopy and close to the main trunk above the scion–rootstock graft; and Ψ_l was taken as the average measured on equal numbers of exposed shaded and sunlit leaves since water flows in parallel to these two groups of leaves (Moreschet *et al.*, 1990).

There are two possibilities for determining R (see Introduction): (i) Ψ is taken as the change in Ψ from before dawn to midday, and the water flux is taken as the average obtained at midday; and (ii)

linear regression of hourly measurements of Ψ on water flux. In order to decide which approach to use, the relationship of sap flow rate to stem Ψ measured at 1.5 h intervals from pre-dawn to late afternoon on the same tree on several dates was examined. Plots of Ψ as a function of sap flow showed that there was hysteresis in the daily curve. Therefore, when a full day of measurements is not available, the regression approach can lead to errors. However, for days when most of the day was measured at regular intervals, the two approaches did not give significantly different results. The first approach (i) was adopted, which was applicable to all the data sets, and it was used to determine the EF R values reported here.

Hydraulic conductance—high pressure flow meter (HPFM) method

Measurements of R using an HPFM (Tyree *et al.*, 1995) were performed in Vermont, USA. Measurements were with de-ionized, degassed water with no additives. Large pressure fittings were manufactured to fit the tree trunks whose diameters ranged from 4 cm to 10 cm. Holes in the trunk left from the sap flow measurements were sealed with screws and rubber washers to prevent leaks. In order to get a good seal, a position on the trunk that was smooth, close to circular in cross-section, and did not have holes from heat pulse measurements was selected. These constraints resulted in differences in the length of trunk measured on each tree. The flow rate into the trunk at high pressure (~ 0.5 MPa) was in the order of 0.25 l min^{-1} , so the HPFM was fitted with a 2 gallon (~ 8.0 l) captive air tank, which was refilled between measurements.

Trees were cut several centimetres above the graft union; the exposed wood of the trunk was shaved with a razor knife, and then attached to the HPFM. The upper part of the tree (i.e. shoot) was perfused through the trunk at high pressure until leaves were visibly waterlogged, i.e. until leaves became dark green and drops of water were seen to exude from the stomata. This usually took less than 30 min. At that point R was monitored until it became steady, and a quasi-steady state (QSS) reading was taken (Bogeat-Triboulot *et al.*, 2002). This was followed by two or three transient measurements. The HPFM was then returned to steady-state mode and all leaves were removed. The same procedure (i.e. QSS and transient measurement) was then repeated. The exposed lower part of the trunk was then shaved and attached to the HPFM for root R measurement. Attempts to make immediate transient measurements were unsuccessful because of non-linearity in the pressure flux plot. This is a typical problem when measuring wood containing a significant amount of air (Nardini and Tyree, 1999; Bogeat-Triboulot *et al.*, 2002). The system was then perfused until a constant R was obtained (after 10–20 min) and then QSS and transient measurements were made. As differences between the QSS and transient measurements were not significant, QSS measurements are reported. Upon completion of the root measurements, QSS measurement continued while the trunk was cut below the graft union. The trunk, which was then 35–40 cm long, was subsequently shortened every few minutes by from 4 to 17 cm while QSS measurement continued. Stem-specific resistivity of the stem section containing the graft union and sections above the graft that belong to the scion were determined from the latter measurements. The length of the stem section containing the graft union averaged 10 cm and varied from 3 cm to 17 cm according to where it was convenient to cut and connect the HPFM fitting. In order to normalize the results, the length of the graft union was taken as 5 cm and, where the graft union stem section measured exceeded 5 cm, R of a section of scion stem of length equal to the excess length was subtracted from the result.

HPFM measurements were made on one tree per day, and a total of eight trees were measured (see Fig. 6). Measurements began in the morning between 09.00 h and 11.30 h, and took 2–3 h to complete.

Leaf area

In the autumn or during HPFM measurement (for trees measured with the HPFM) all leaves were harvested from the trees. These were weighed and at least three subsamples of at least 100 g each were taken for determination of the ratio of leaf area to fresh weight. Subsample leaf area was determined with Li-Cor (model LI-3100; Lincoln, NE, USA) and Delta-T image analysis and conveyor belt (Cambridge, UK) leaf area systems. The average ratios were then used to determine total leaf area for each tree.

Statistics

Analysis of variance (ANOVA) was with the GLM routine of SAS (SAS Institute, 1982) where rootstock, place, and year were defined as class variables. Linear interactions between the classes were tested. Differences between means were considered significant when type III sum of squares met the *F*-test criterion at <0.05 probability. When ANOVA showed that significant differences existed between means, the Duncan multiple range test (DMRT with $\alpha=0.05$) was used to determine which means were significantly different.

Conductance, conductivity, resistance, and resistivity

Conductance and resistance are reciprocals, and express the water transport ability of a portion of the plant irrespective of its length, in units of $\text{kg m}^{-2} \text{MPa}^{-1} \text{s}^{-1}$ and $\text{MPa m}^2 \text{s kg}^{-1}$, respectively. Conductance (and resistance) expressed relative to leaf area (K_l and R_l) and cross-sectional area of conductive tissue (i.e. specific conductance) have different implications (Tyree and Ewers, 1991; Tyree, 1999); the former expresses the ability of the plant to supply water to the leaves, and the latter expresses the hydraulic ability of the stem. Conductivity and resistivity (k and r) are also reciprocals, but these express the hydraulic properties of a unit length of conductive tissue, with units of $\text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$ and MPa m s kg^{-1} , respectively. Since water flux in the plant, as measured in this study, is through a series of resistances from soil to shallow roots to stem (and through the graft union) to leaves, the total resistance is the sum of the resistances. It is therefore convenient to present the results as resistance and resistivity, and when these are compared with values of conductance previously reported, those data have been converted to resistance.

Determination of the cross-sectional area of conductive tissue is problematic since the xylem may not be uniform, as indicated by the decrease of sap velocity with depth in trunks of apple trees (Cohen and Naor, 2002). In the trees studied, sap velocity was measured to a depth of 44 mm in the xylem, and the relationship of sap velocity to depth showed that there was no non-conductive heartwood. Therefore, conductance was not expressed relative to conductive tissue but relative to trunk (i.e. stem) cross-sectional area. This is referred to as stem-specific conductance and its inverse, resistance (K_s and R_s).

Results

Soil to stem resistance—EF method

$R_{\text{soil-stem}}$ is the sum of the soil resistance at the soil-root interface, radial and axial resistances in the root, and resistance of the stem, including the rootstock-scion union. During the drought in the summer of 2001 in Vermont, $R_{\text{soil-stem}}$ increased as Ψ_{pd} decreased, apparently due to the increasingly large R of the drying soil. The increases exceeded the differences between

rootstocks. During the summer of 2002, Ψ_{pd} was higher and $R_{\text{soil-stem}}$ remained relatively low. Since for the dry conditions of 2001 soil to stem and total R were more influenced by soil water than rootstocks, they are not reported.

Stem- (R_s , Fig. 1A) and leaf- (R_l , Fig. 1B) specific resistance of the soil to stem pathway of three rootstocks, M9, MM106, and MM111, were measured in both countries during two summers (Fig. 1) and additional data for the Israeli site are available from a previous study (Table 2). Because of the similarity between MM106 and MM111 in both genetics and vigour (Table 1), they are presented as a comparison with the dwarfing M9 rootstock. Significant differences between rootstocks for $R_{\text{s,soil-stem}}$ (Fig. 1A) were not found in any of the cases, while mean $R_{\text{l,soil-stem}}$ (Fig. 1B) was consistently greater in M9, significantly so in Israel in 2002. Significant differences were found between the sites and years of measurement; $R_{\text{s,soil-stem}}$ ranged from 6.1 to 17.2, and $R_{\text{l,soil-stem}}$ from 9.2×10^3 to $4.7 \times 10^4 \text{ MPa m}^2 \text{s kg}^{-1}$.

Root to stem resistance—EF method

$R_{\text{root-stem}}$ is the sum of the axial root R from the point of measurement in the large roots (i.e. where the sucker grew out of the root) to the stem, and that of the stem and the

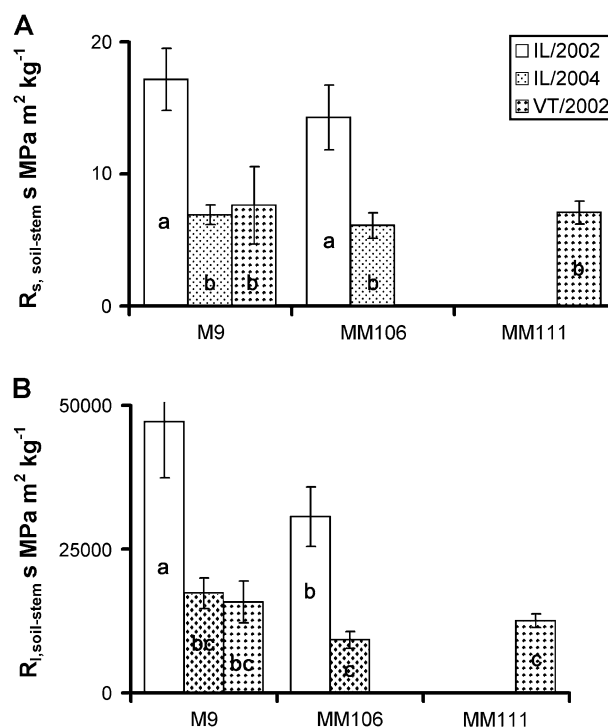


Fig. 1. Stem- (A) and leaf- (B) specific EF hydraulic resistance for the soil to scion stem pathway. Measurements are for the dwarf M9 and the vigorous MM106 (Israel) and MM111 (Vermont) rootstocks during three summers. Vertical bars indicate \pm SEM. ANOVA for each set of data indicated significant differences between rootstocks ($P < 0.01$). Letters indicate significant classes from DMRT ($P < 0.05$).

Table 2. Stem- and leaf-specific hydraulic resistance ($s \text{ MPa m}^2 \text{ kg}^{-1}$, mean \pm SE) measured by the EF method during the experiment. Numbers with the same letter are not significantly different at $\alpha=5\%$ (DMRT). Levels of significance ($P > F$) are from ANOVA.

Place	Year	Class	Rootstock	$R_{s, \text{ soil-stem}}$	$R_{l, \text{ soil-stem}}$	$R_{s, \text{ stem-leaf}}$	$R_{l, \text{ stem-leaf}}$	Soil-stem/ Soil-leaf
Israel	2002	Dwarf	M9	17.1 \pm 2.4 a	47 160 \pm 9785 a			
Israel	2004	Dwarf	M9	6.91 \pm 0.73 cd	17 322 \pm 2668 bcd			
Israel ^c	1998	Dwarf	M9	3.69 \pm 0.61		3.26 \pm 0.63		0.53
Vermont	2001	Dwarf	M9	^a	^a	2.92 \pm 0.17cd	9891 \pm 1668 bc	
Vermont	2002	Dwarf	M9	7.62 \pm 2.94 cd	15 797 \pm 3659 bcd	2.70 \pm 0.56 cd	6153 \pm 820 c	0.74
Vermont	2001	Dwarf	CG202	^a	^a	3.45 \pm 0.30 bc	15 619 \pm 1324 a	
Vermont	2002	Dwarf	CG202	5.31 \pm 1.58 d	21 576 \pm 4822 bcd	2.46 \pm 0.35 cd	10 240 \pm 170 b	0.68
Vermont	2001	Semi-dwarf	M7a	^a	^a	3.66 \pm 0.44 bc	14 784 \pm 1678 a	
Vermont	2002	Semi-dwarf	M7a	6.15 \pm 0.44 d	17 858 \pm 220 bcd	3.46 \pm 0.28 bc	10 073 \pm 629 bc	0.64
Vermont	2001	Semi-dwarf	CG30	^a	^a	1.65 \pm 0.17 d	6965 \pm 1236 bc	
Vermont	2002	Semi-dwarf	CG30	5.80 \pm 0.13d	26784 \pm 1111bc	3.33 \pm 0.10 bc	15 415 \pm 1089 a	0.64
Israel	2002	Semi-dwarf	MM106	14.3 \pm 2.5ab	30641 \pm 5179b			
Israel	2004	Semi-dwarf	MM106	6.10 \pm 0.97 d	9211 \pm 1469d			
Israel ^c	1998	Semi-dwarf	MM106	4.22 \pm 0.31		3.92 \pm 0.48		0.52
Vermont	2001	Vigorous	MM111	^a	^a	3.45 \pm 0.40 bc	8793 \pm 1028 bc	
Vermont	2002	Vigorous	MM111	7.08 \pm 0.87 cd	12 568 \pm 1194 cd	3.62 \pm 0.27 bc	6732 \pm 770 bc	0.66
Vermont	2001	Vigorous	CG934	^a	^a	6.13 \pm 0.44 a	16 054 \pm 1471 a	
Vermont	2002	Vigorous	CG934	12.0 \pm 1.2 bc	18 100 \pm 1576 bcd	4.64 \pm 0.36 b	7069 \pm 532 bc	0.72
Significance ($P > F$)								
All				<0.001	<0.001	<0.001	<0.001	
Rootstock				<0.05	<0.05	<0.001	<0.001	
Place				<0.001	<0.001	^b	^b	
Year				<0.001	<0.001	n.s.	<0.001	
Rootstock \times place				n.s.	n.s.	^b	^b	
Rootstock \times year				^b	^b	<0.01	<0.001	

^a Data for the soil to stem pathway measured in Vermont in 2001 have been omitted. See text.

^b Not applicable.

^c Data measured in a different orchard on the same Kibbutz. EF methodology was the same but leaf area was determined by gap fraction inversion, so R_l is not included. For details see Cohen and Naor (2002). These data were not included in the statistical analysis.

graft union. These measurements (Fig. 2A, B) were made in M9 and MM106 during two summers in Israel. In both cases, $R_{\text{root-stem}}$ in M9 was higher, but large differences were observed for M9 in the two summers, with the value for 2002 being >4 times that observed in 2004. For MM106, values obtained in the two summers were not significantly different, and $R_{s, \text{ root-stem}}$ and $R_{l, \text{ root-stem}}$ averaged 1.0 and 2000 $s \text{ MPa m}^2 \text{ kg}^{-1}$, respectively.

$R_{\text{root-stem}}$ represented 13–22% of $R_{\text{soil-stem}}$ for MM106 and 30–45% for M9 (Fig. 2C). Thus, in these well-watered situations, R through the root and across the graft union for M9 is comparable in magnitude with R from the soil to the large-root xylem.

Stem to leaf resistance—EF method

R_s and R_l from stem to leaf for the six rootstocks was measured in two summers in Vermont (Fig. 3A, B). Measurements made in Israel in 1998 in a previous study (Cohen and Naor, 2002) gave results similar to those from Vermont, and are given here for comparison (Table 2). Significant differences were found between rootstocks and between the years (Table 2), but the only trend observed was a significant positive correlation between $R_{s, \text{ stem-leaf}}$ and rootstock vigour (Fig. 3A). The lowest $R_{s, \text{ stem-leaf}}$ was found for the semi-dwarf, CG30, and the highest for the

largest (and most vigorous) trees, CG934. The pooled relationship between $R_{s, \text{ stem-leaf}}$ and trunk cross-sectional area (A in m^2 , Fig. 3C) for the two years was $R_{s, \text{ stem-leaf}} = 369 A + 1.96$ ($r^2=0.54$; $P < 0.01$). For the soil to stem and total soil to leaf pathways, measured in 2002, R_s was also significantly ($P < 0.05$) positively correlated with scion trunk cross-sectional area (Fig. 4) and not with tree leaf area. No significant relationships were found between vigour and R_l for any of the pathways.

The ratio of resistance in the soil–stem to the stem–leaf pathway ranged from 0.52 to 0.74 (Table 2). The ratio was not significantly related to the vigour categories.

HPFM measurements

HPFM measurements were used to determine R_l (Fig. 5A) and percentage of R (Fig. 5B) for the different parts of the tree for each of the rootstocks, where results are from either one individual tree or an average of two trees. In all cases the part of the stem containing the graft union comprised only a small part of the resistance to water flow. As expected, the highest R occurred in the root system, which constituted approximately half of the total R , and the combined R of stem and leaves was comparable. Similarly, Landsberg *et al.* (1976) reported that root resistance accounted for 40–74% of the total

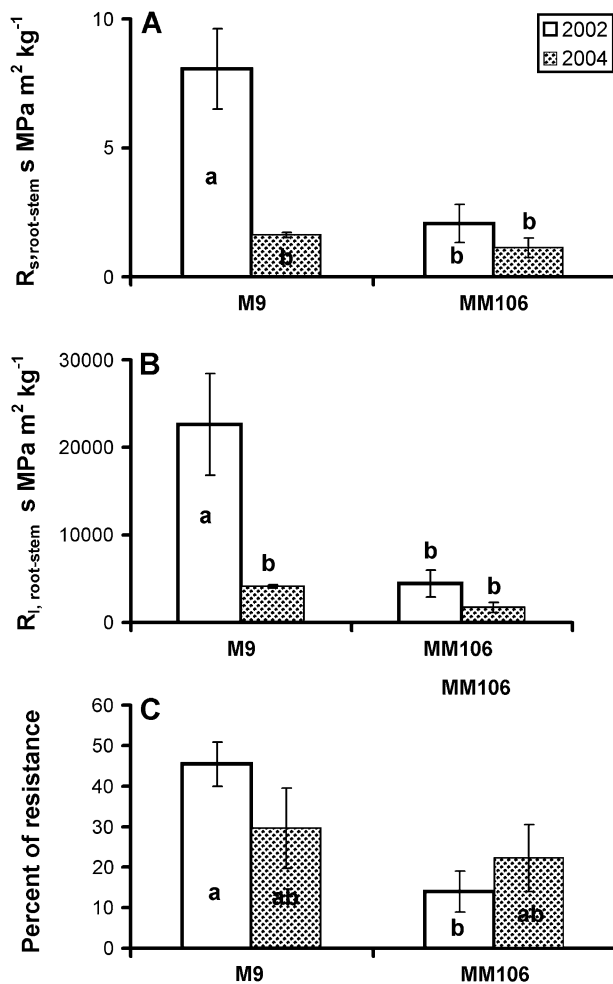


Fig. 2. Leaf- and stem-specific EF hydraulic resistance from root to scion stem (A, B), and expressed as a percentage of the total resistance from soil to scion stem (C) for M9 and MM106 measured in Israel during two summers. Vertical bars indicate \pm SEM. ANOVA for each set of data indicated significant differences between rootstocks (for A and C, $P < 0.05$; for B, $P < 0.01$). Letters indicate significant classes from DMRT ($P < 0.05$).

plant resistance in young apple trees. In the present case, the leaf R includes that of the petioles, since the leaves were removed at the base of the petioles. Partitioning of R between the four tree parts did not reveal any clear relationship with rootstock vigour class.

EF and HPFM measurements made on the same trees were compared for the lower (root–stem) and upper (stem–leaf) parts of the tree (Fig. 6A, B). In all except one case (i.e. the shoot of CG934), EF R was much higher than that obtained with the HPFM. The average ratios of HPFM to EF values of R were 0.42 and 0.59 for the lower and upper parts of the tree, respectively. No correlation between the ratios and rootstock vigour was apparent.

Resistivity of graft union and non-graft union trunk sections was determined for six stems. In dwarf trees, leaf-specific resistivity of the graft (Fig. 7) was several times

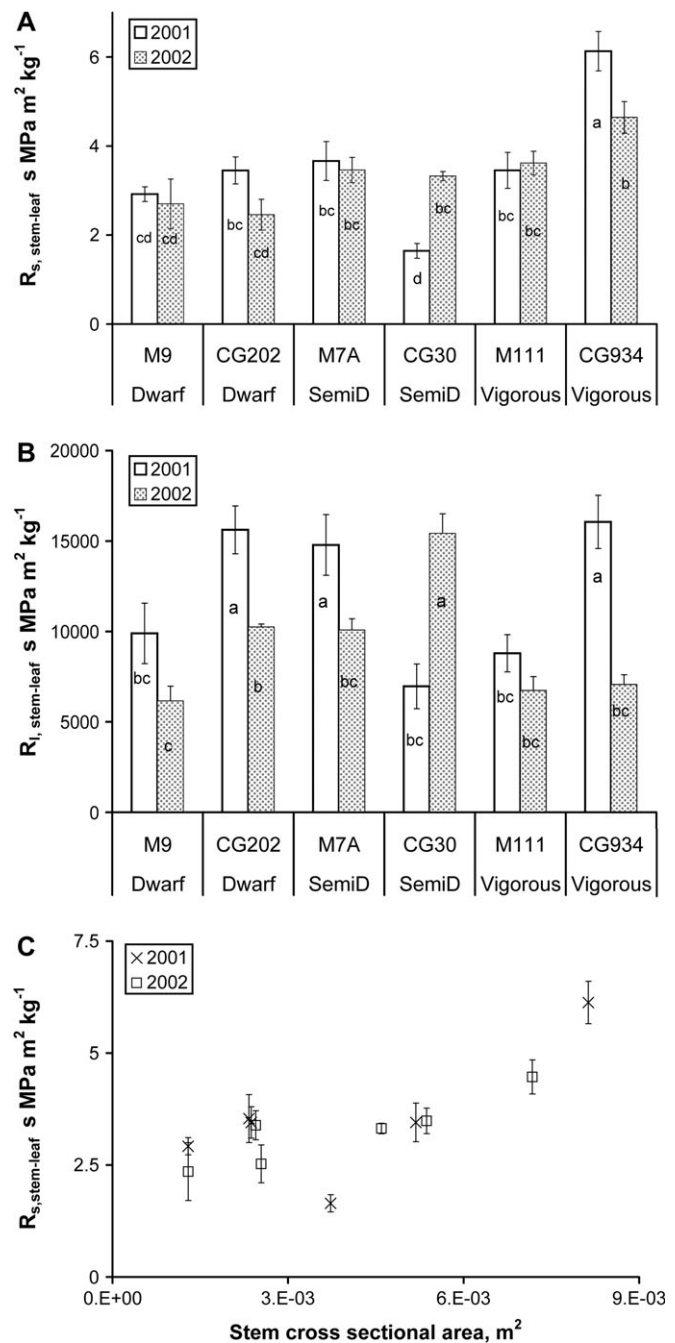


Fig. 3. Stem- (A, B) and leaf- (C) specific hydraulic EF resistance measured for the scion stem to leaf pathway. Measurements from the Vermont rootstock trial during two summers. Resistance is plotted for each rootstock (A, C), and as a function of relative stem cross-sectional area (B). Vertical bars indicate \pm SEM. ANOVA for each set of data indicated significant differences between rootstocks ($P < 0.01$). Letters indicate significant classes from DMRT ($P < 0.05$).

that of the scion stem, in the semi-dwarfs graft union and scion had similar resistivity, and in the one vigorous tree resistivity of the graft union was much lower than that of scion stem. Resistivity of the scion stem sections was not significantly different on different rootstocks.

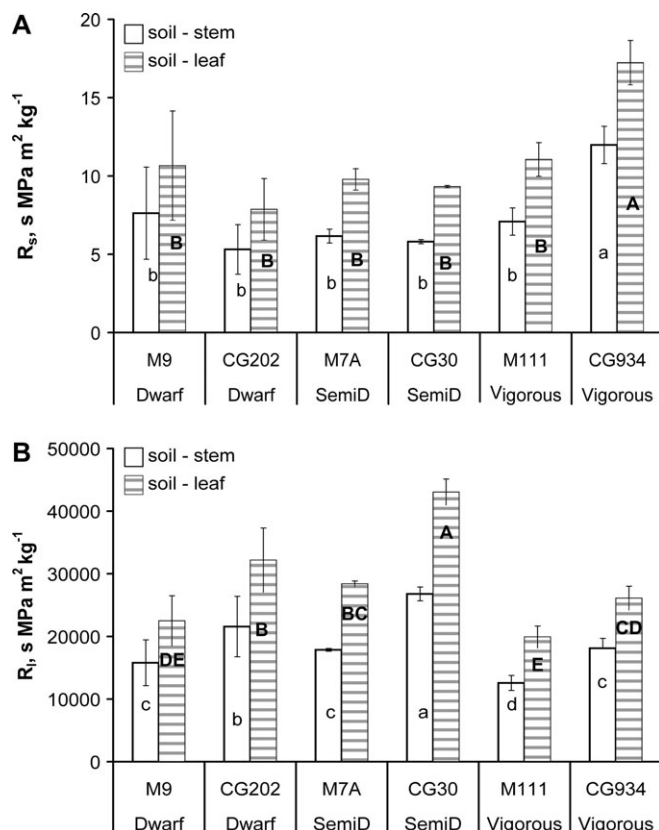


Fig. 4. Stem- (A) and leaf- (B) specific hydraulic EF resistance measured for the soil to scion stem and full soil to leaf pathway. Measurements from the Vermont rootstock trial in 2002. Resistance is the average for each rootstock. Vertical bars indicate \pm SEM of two trees measured on two days. ANOVA for each set of data indicated significant differences between rootstocks ($P < 0.01$). Letters indicate classes from DMRT ($P < 0.05$).

Discussion

Accuracy and precision of EF measurements of hydraulic resistance

EF R is derived from measurements of leaf water potential, sap flow rate, and leaf area or trunk cross-sectional area. The errors in each of these parameters may add up. The least accurate are sap flow rate and leaf area. Leaf area meter measurements are accurate to 3%, while the use of the relationship between subsample wet weight and area introduces another error of the same magnitude, based on standard errors of the subsamples, giving an estimated accuracy of 5–10% for individual tree leaf area.

The heat pulse technique, as implemented in this study, gives accurate measurements of sap flux density (Cohen, 1994) and compared favourably with an open chamber method in apple trees (Dragoni *et al.*, 2005). One source of error, i.e. that due to inaccuracy of the distance between heater and probe (Jones *et al.*, 1988), was minimized here with the use of a drill guide that gave accurate bores for the full probe length (see Materials and methods). The

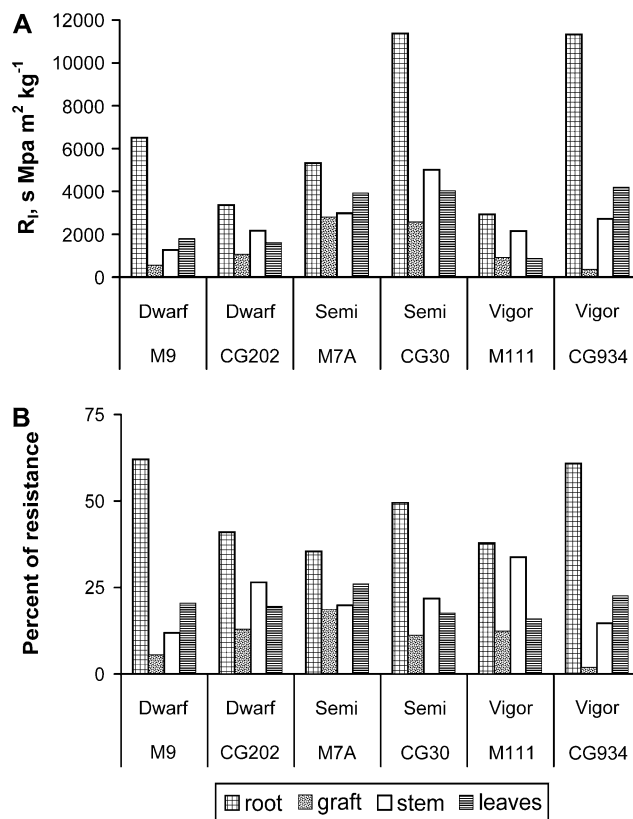


Fig. 5. Leaf-specific (A) and percentage (B) resistance in the different parts of the tree, from HPFM measurements of full-sized 11-year-old trees from the Vermont rootstock trial. Semi, semi-dwarf; vigor, vigorous. $n=1$.

physical properties of the wood influence heat pulse measurements. However, since all sap flow measurements in the current study were made in wood of the scion Golden Delicious variety in Israel and the Liberty variety in Vermont, differences in thermal transport properties of the wood are unlikely to have introduced bias in the results when comparing results within each country.

Sap flux density is highly variable from tree to tree, and can also vary depending on the azimuth at which the probe is inserted in the trunk (Cohen and Naor, 2002; Dragoni *et al.*, 2005). Cohen (1991) found the coefficient of variation (CV) for measurements in different citrus trees in the same treatment to be 0.3. In the present case, since the measurements were averages of 2–8 trees per vigour (in Vermont and Israel, respectively), the accuracy of sap flow is probably not better than 15%. Summing these two errors gives an estimate of ~25% for the accuracy of average of leaf-specific R estimated by the EF method in this study.

In the summer of 2001, four trees, two M111 and two CG934, were measured on four days. The variability in these measurements can give an indication of the precision of the EF measurements. R in the soil to stem and stem to leaf pathways was determined independently for

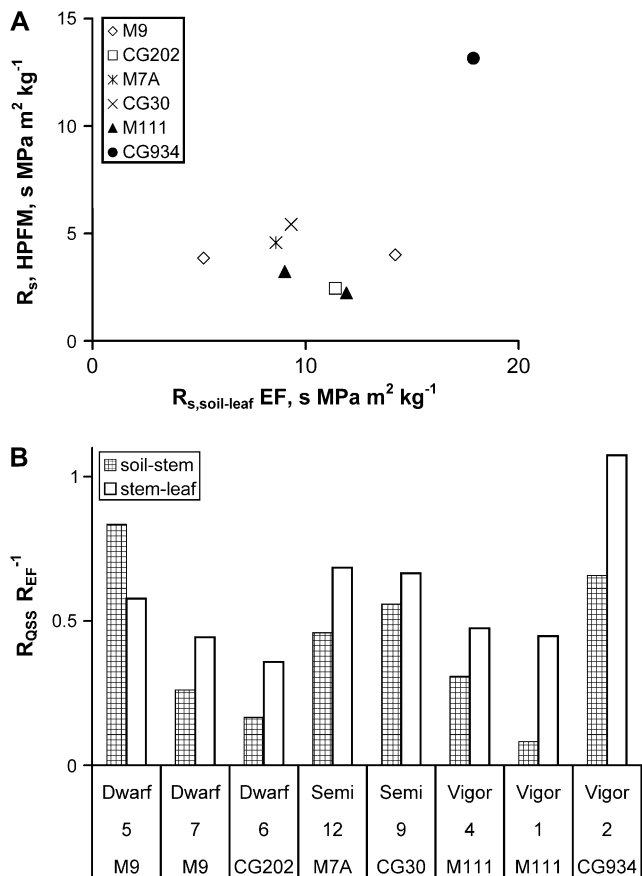


Fig. 6. (A) Comparison between total plant stem-specific hydraulic resistance measured by the EF and HPFM methods on eight trees from the Vermont rootstock trial in 2002 ($n=1$). Rootstock type is indicated. (B) Ratio of HPFM (QSS) to EF measurements of hydraulic resistance for the soil–stem and stem–leaf pathways. Data points were computed from measurements made on the individual trees that were harvested in the autumn of 2002. Size class, tree serial ID, and rootstock are noted. Semi, semi-dwarf; vigor, vigorous.

each of the days. The average CV for the four day averages for the four trees was $25 \pm 1\%$ and $25 \pm 5\%$, for the soil to stem and stem to leaf pathways, respectively. The CV for the averages of the two years of measurement of R from stem to leaves for M9 was 11% (Table 2). It is therefore expected that the CV for measurement of R with the EF technique used in this study is between 10% and 25% and, since data presented are usually an average of 2–4 measurements, their confidence interval is in the order of 10% of the mean.

Magnitude of hydraulic resistance and resistivity—comparison with other reports for apple

Several studies have reported hydraulic data for apple trees that, after manipulation, can be compared with the present measurements. Cohen and Naor (2002; Tables 2, 3) used the same EF method during one summer (1998) and reported values of similar magnitude. The current study improves on that previous one in that more replicate

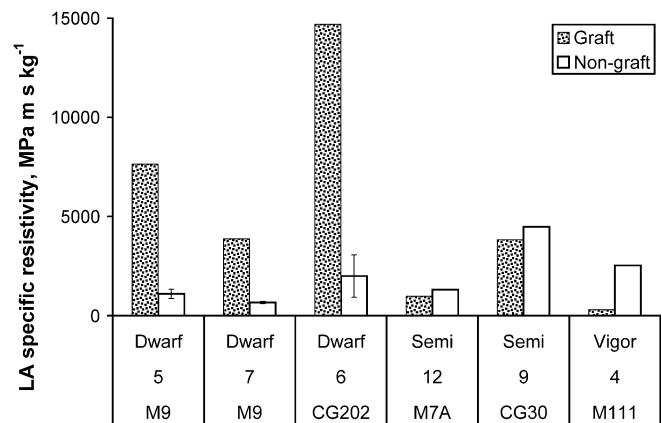


Fig. 7. HPFM measurements of leaf-specific stem resistivity for graft union and scion. Measurements were made on sections of the main trunk of individual fully grown trees. Rootstock type and tree ID are given. Where $n > 1$, vertical bars indicate $\pm \text{SEM}$.

measurements were made (i.e. two seasons in Israel and two in the USA), and leaf area measurement here was measured directly, while the previous study used gap fraction analysis, whose accuracy is only $\sim 20\%$ (Welles and Cohen, 1996; Cohen *et al.*, 1997) and can be influenced by canopy clumpiness, which may not be constant from tree to tree (Cohen *et al.*, 1995).

R_s components for a full-sized orchard-grown Cox's Orange Pippin tree (Table 3), reported by Landsberg *et al.* (1976), were close to the present values (Table 2; Figs 3, 4), but R_1 values were an order of magnitude lower. Their experiment was performed in October, and although they noted that it was before leaf fall, the leaf area may well have been less than during the main growing season. Components of R_1 for 2-year-old potted trees of the Golden Delicious variety (Landsberg *et al.*, 1976; Table 3) were an order of magnitude higher than those in the present study. There is evidence that under low evaporative demand when water supply is not a limiting factor, leaf-specific hydraulic resistance can be higher than when water supply is limiting (Li *et al.*, 2005). It is suggested that in the latter study, the potted trees might have been grown in such conditions, leading to high leaf-specific resistance.

Atkinson *et al.* (2003) measured *in vitro* conductivity (i.e. conductance per unit length) at low pressure (6 kPa) of sections of root and stem cut under water for three apple rootstocks from grafted and ungrafted trees. Their results, converted to leaf-specific resistivity, for scion stem (which ranged from 970 to 1900 s MPa m kg^{-1}) and the graft union (340–4170 s MPa m kg^{-1}) are close to the present HPFM measurements (Fig. 7). They also found through staining that only a fraction of the stem is active in water transport. The latter, together with the fact that the present *in vivo* measurements of R were higher than those made at high pressure (Fig. 6b), suggests that a significant portion of the xylem in the trees under study here may have been dysfunctional, possibly due to

Table 3. Comparison of apple stem- and leaf-specific hydraulic resistance ($s \text{ MPa m}^2 \text{ kg}^{-1}$) values measured with similar EF methodology

Source	Species or apple variety	Rootstock	R_s , soil–stem	R_l , soil–stem	R_s , stem–leaf	R_l , stem–leaf
Current study	See Table 2		5.3–17	9200–47 000	1.7–6.1	6200–16 000
Cohen and Naor (2002)	Apple–Golden Delicious	M9	4.1	11 000	2.8	7600
		MM106	4.2	6500	3.9	6100
Landsberg <i>et al.</i> (1976)	Apple–Cox’s Orange Pippin–11 years old		7.7	620	6.2	770
	2-year-old potted trees			225 000		20 2000

cavitation. However, if cavitation is significant, then their measurements at low pressure, at which refilling of cavitised vessels is not believed to occur (Sperry *et al.*, 1988), should have given higher resistance than the present HPFM measurements. That was not the case. Atkinson *et al.* (2003) also reported that staining was less in the scion stem of two dwarfs than in the more vigorous MM106, which might be taken as an indication of more xylem dysfunction. The latter is not supported by the ratios of *in vivo* high pressure to *in vitro* conductance shown in Fig. 6B. They concluded that stem-specific R was higher in dwarfs, while the present *in vivo* measurements show a significant decrease with decreasing vigour (Figs 3, 4).

One important difference from Atkinson *et al.* (2003) is that they measured young stems, while fully grown tree stems were measured in the present study. Since for the latter, stem cross-sectional area is highly positively correlated with vigour (and is actually used as a measure of vigour), the correlation of vigour with stem-specific R may indicate that a smaller percentage of the stem is active in the vigorous trees with the large stems. When trees are young and stem cross-sectional area of the different rootstocks is more similar, as may have been the case for Atkinson *et al.* (2003), the situation may be different.

Rootstock hydraulic resistance—comparisons with other species

Nardini *et al.* (2006) reported HPFM measurements of R for dwarf and vigorous selections of one olive cultivar, *Olea europaea* cv. ‘Leccino’. Grafted and non-grafted 3-year-old saplings 360 d and 450 d after grafting were measured. They found that the smaller root systems of the dwarf saplings had significantly higher resistance than those of the more vigorous saplings, but when root resistance was expressed relative to the leaf area (i.e. as R_l) differences between vigours were small. Their values of $R_{l, \text{root–stem}}$ not including the graft ranged from 8000 to 12 000 $s \text{ MPa m}^2 \text{ kg}^{-1}$ and of $R_{l, \text{stem–leaf}}$ including the graft ranged from 3000 to 10 000 $s \text{ MPa m}^2 \text{ kg}^{-1}$. These values are very close to the present values (Fig. 5A).

Basile *et al.* (2003a, b) reported HPFM measurements of peach trees on three rootstocks of different vigours. Their measurements gave $R_{l, \text{root–stem}}$ values of 4000–5000 $s \text{ MPa m}^2 \text{ kg}^{-1}$ and $R_{l, \text{stem–leaf}}$ values of 13 000–

17 000 $s \text{ MPa m}^2 \text{ kg}^{-1}$, which is also within the range of the present measurements.

They found that diurnal changes in stem water potential and differences in leaf-specific R of the root and graft system were negatively correlated with differences in shoot elongation rates. The differences in R that they observed were of the order of 22–26%, which is smaller than the 95% confidence intervals (i.e. 2 SEMs) for some of the means measured in the current study. Evaluation of the accuracy and precision of the EF measurements of resistance (see above) indicates that if differences in R between apple rootstocks were greater than 20%, as found by Basile *et al.* (2003a, b) in peach trees, it would have been expected to have found them in the current study, and this was not the case.

Differences between HPFM and EF measurements

HPFM measurements of R were significantly lower than those for the EF method in almost all cases (Fig. 6). For the root system, where apparent air in the wood prevented measurements of R until after perfusion, higher values of R might be expected due to accumulation of ions in the roots during perfusion (Tyree *et al.*, 1995). However, for the roots, the HPFM still gave lower values than the EF method (Fig. 7). Tsuda and Tyree (2000) made extensive comparisons between the EF and HPFM methods for annual plants and small tree branches and found that results are usually similar, but Rieger (1989) found that, in peach, high pressure measurements sometimes gave significantly lower resistance than low pressure measurements. He hypothesized that the difference can be an indication of xylem dysfunction due to cavitation in the xylem. The air-filled xylem is rehydrated under high pressure, thus causing the decreased resistance. It is assumed that in the large trees measured in the current study the discrepancy between the HPFM and EF measurements (Fig. 6) can be explained in this way.

R and rootstock vigour

Of the four sets of EF measurements, only one, that for Israel in 2002, supports previous findings (Cohen and Naor, 2002; Atkinson *et al.*, 2003) that leaf-specific R in the soil to scion stem pathway for trees on the dwarf M9

rootstock is significantly higher than that for more vigorous MM106 and MM111 rootstocks (Table 2; Figs 1B, 6B), especially for the pathway from large roots to scion stem (Fig. 2B). For the other data sets, and from a larger set of six rootstocks of different vigours (Fig. 4), some significant differences in resistance were found, but there was no consistent negative relationship between rootstock vigour and R , whether on a leaf-specific or stem-specific basis. Several HPFM measurements of R did not show any other patterns, but measurements of stem sections with and without graft unions showed that resistivity of the graft union is larger at lower vigour.

Resistance of the graft union comprised only a small part of the total plant R . Therefore, it is concluded that variations in total leaf- or stem-specific hydraulic resistance cannot be the only explanation for the differences in observed vigour of the apple rootstocks.

Conclusions

Examination of a series of mature apple trees on rootstocks with a range of vigours indicated that stem- and leaf-specific R in the soil to stem, stem to leaf, and total soil to leaf pathway were not consistently negatively correlated with vigour. The only consistent gradient in hydraulics observed was an increase in stem-specific R (i.e. a decrease in conductance) with increasing vigour (Figs 3A, C, 4A). R differences between rootstocks were smaller than those caused by inadequate irrigation. Even so, the resistivity of graft union portions of the stem was found to decrease with increasing vigour (Fig. 7). This may influence the transport of water and other elements across the graft union, and may therefore be involved in the dwarfing mechanism.

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